

10 Visual cognition in deep-sea cephalopods: what we don't know and why we don't know it

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10.1 The other cephalopods

A quick glance at the recent cephalopod literature, or even at the chapters of this book, tells us that when we talk about cephalopod cognition we are really considering cognition in a handful of genera. There can be no argument that studies of these animals have led to remarkable results that have challenged the traditional view of invertebrate intelligence. Yet when we consider that less than 10 species of cephalopod are commonly seen as the focus of behavioral studies, let alone in studies specifically about cognition, it becomes apparent that claims regarding the cognitive capabilities of cephalopods are generalizations drawn from work on a handful of genera. The majority of the 800 or so described species of cephalopod do not share the neritic and near-shore benthic habitats of the taxa with which we are most familiar; virtually unknown in terms of their behaviour and ecology, these species inhabit a different world in the deep, dark waters of the open ocean (Figure 10.1).

In this chapter, we introduce and discuss the neglected cephalopods of the deep sea, many of which are not so distantly related to the species with which we are familiar, but whose existence in the deep sea has little in common with the complex reefs and near-shore habitats associated with taxa such as *Octopus* and *Sepia*. What effect might these differences in ecology have on the cognitive abilities of deep-sea cephalopods compared with their shallow water relatives? Chapter 9 of this volume (by Zylinski & Osorio) explored what we can deduce about cuttlefish visual cognition from the body patterns they use for camouflage. In this chapter we revisit the theme of making inferences about visual perceptive and cognitive abilities via body patterning in the handful of epipelagic and mesopelagic species that have been studied to date. Prior to that, we consider how the cognitive needs of these animals might differ from those of near-shore or shallow benthic environments. We explore what is known about the potential for visual cognition in deep-sea cephalopods and discuss why we know so little. Readers might find this chapter heavier on natural history and observation than the others in this book, but we hope that it will serve as a reminder that most cephalopods are essentially unknown beyond their descriptions.

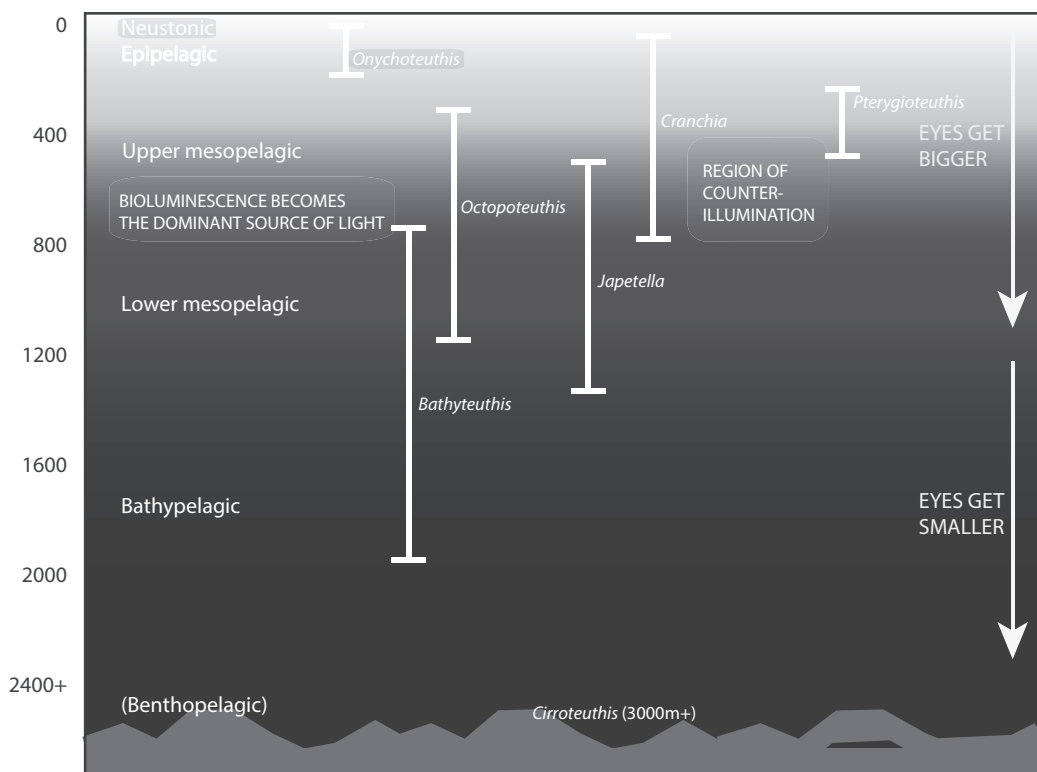


Figure 10.1 Approximate depths in metres of habitat zones for clear oceanic waters. Benthopelagic realm is close to the ocean floor at any depth of the pelagic realm. Vertical lines show approximate depth ranges for some of the species referred to in this chapter, taken from daytime trawl data for adults (Arkhipkin, 1996; Arkhipkin & Nigmatullin, 1997; Roper & Young, 1975).

10.2 Why do we know so little about the other 95%?

Although notoriously ‘moody’ (Talbot & Marshall, 2010) the coastal cephalopod taxa with which we are familiar (e.g. *Sepia* and *Octopus*) can be hatched and/or kept in the laboratory with some level of expertise and patience (e.g. Domingues, Dimarco, Andrade & Lee, 2005; Forsythe, Lee & Walsh, 2002). This has led to the volume of well-controlled visual behavioural research we have for these animals (e.g. Barbosa, Allen, Mäthger & Hanlon, 2012; Chiao, Chubb, Buresch, Siemann & Hanlon, 2009; Mäthger, Chiao, Barbosa & Hanlon, 2008; Shashar, Rutledge & Cronin, 1996; Shohet, Baddeley, Anderson, Kelman & Osorio, 2006; Zylinski, Osorio & Shohet, 2009), supplemented by field observations and experiments where data can be obtained with relative ease with scuba (e.g. Hall & Hanlon, 2002; Zylinski, How, Osorio, Hanlon & Marshall, 2011) or even by snorkeling (e.g. Hanlon, Forsythe & Joneschild, 1999). Behavioural observations, let alone controlled behavioral experiments, are few and far between for mesopelagic animals. Collecting animals from mesopelagic depths requires either the use of specialized trawl nets or undersea vehicles (e.g. a remotely operated vehicle (ROV))

or manned submersible). ROVs and submersibles enable *in situ* observations of animals, which have greatly improved our knowledge of interactions, behaviour and physiology of deep-sea animals, as well as enabling the gentle capture of specimens (Hunt & Seibel, 2000; Robison, 2004; Vecchione & Roper, 1991). However, experimental behavioural biology requires a rigorous framework beyond these natural history observations, and there are some concerns about the influence of motor vibrations and viewing lights on *in situ* behavioural observations (for example, animals living in perpetual near-darkness are probably literally and permanently blinded by these lights). The collection of animals using trawl nets has been aided by the use of thermally-insulated and light-tight closing cod ends (Childress, Barnes, Quetin & Robison, 1978), which enables the recovery of specimens in collection-depth temperatures and light conditions, and prevents excessive mechanical damage. However, in both cases, there is no guarantee that the animals required for a planned experiment will be caught. Weeks at sea can be spent in frustration as each trawl returns to the surface without the target taxa for a specific study. Luck and patience are both critical for the deep-sea biologist!

Trends in data from vertebrates and hymenopteran insects suggest that certain lifestyles and the need to deal with specific tasks predispose the evolution of complex behavior. Ecological complexity is generally associated with cognition, be it the need to forage for cache-specific foods (e.g. Clayton, Dally & Emery, 2007; Hills, 2006), navigate using cues and landmarks (e.g. Collett & Collett, 2002) or interact with conspecifics (e.g. Bergman, Beehner, Cheney & Seyfarth, 2003; Grosenick, Clement & Fernald, 2007). The ecology of shallow-water, benthic species of cephalopods such as members of *Sepia* and *Octopus* is such that we see clear evidence for complexity in their life histories: octopuses move through complex rocky reef or coral habitats to forage for food (Forsythe & Hanlon, 1997; Hanlon, Forsythe & Joneschild, 1999) and navigate to and from their lairs (Mather, 1991); cuttlefish signal to conspecifics when hunting and during courtship (Hall & Hanlon, 2002; Langridge, Broom & Osorio, 2007; Zylinski, How, Osorio, Hanlon & Marshall, 2011). Species from both genera are well known for the complex body patterns they employ for both signalling and camouflage (Hanlon & Messenger, 1988; Packard & Sanders, 1971).

The mesopelagic habitat offers a different set of ecological requirements: animals can pass their entire lives without coming in contact with any abiotic structure, with hundreds (if not thousands) of metres of water above and below them. Underwater light decreases exponentially with depth, and by 150 m in clear, oceanic water more than 99% of surface light has been scattered or absorbed (Jerlov, 1976) (this said, it should be noted that this can result in surprisingly bright conditions in which the human eye can still function perfectly well). Many species live at greater depths where the amount of downwelling light is so small that it is no longer useful for vision, and here biological light (bioluminescence) is used in many capacities such as signalling, hunting and camouflage (e.g. silhouette reduction via counterillumination) (Haddock, Moline & Case, 2010). Temperatures here tend to be cold (typically between 0 and 6°C) and constant due to the lack of mixing with surface waters (Robison, 2004). The mesopelagic habitat is virtually globally continuous, with the same species found in similar conditions around the world, with absolute depths changing with corresponding differences in temperature, oxygen minimum zone depths and light levels.

In the vast three-dimensional habitat that is the deep-sea pelagic realm, the diversity and quantity of animals decrease in parallel with depth. It is renowned for being a hard place to find a mate, and many non-broadcast spawning deep-sea taxa have evolved unusual reproductive methods, such as male parasitism of females in deep-sea anglerfish (Marshall, 1958). Cephalopods also appear to use some quirky tactics to maximize the chances of reproduction when solitary individuals meet. For example, males of the mesopelagic squid *Octopoteuthis* apparently mate (implant sperm packages) indiscriminately when they encounter both males and females of the same species, presumably because sex differences are hard to determine in low-light conditions and the cost of failing to mate given the opportunity is high (Hoving, Bush & Robison, 2012).

There is also a trend for relative eye size of many taxa to increase as light gets dimmer from the surface waters to the lower-mesopelagic realm, where the downwelling surface light can still be useful if the eye is sensitive enough (Figure 10.1). In the bathypelagic zone (below ~1000 m) the trend reverses, and eye size tends to decrease as ambient light not detectable. In general, eyes in the mesopelagic realm are either designed to maximize the possible light capture and make use of the small amounts of light available at the cost of reducing spatial acuity, or they are optimized to detect point sources (to enable them to see flashes of bioluminescence) at the cost of reduced sensitivity to the ambient light (Warrant & Locket, 2004). Aside from such general trends, evolution has found varied and novel ways to obtain visual information in dim light, and the cephalopods offer some of the most interesting of these. Take, for example, the deep mesopelagic squid *Histioteuthis* (Figure 10.2), which has highly asymmetrical eyes and correspondingly asymmetrical optic lobes (Maddock & Young, 1987; Wentworth & Muntz, 1989). This animal has a large left eye, probably specialized for gaining information from the dim downwelling light as the animal swims on its side with this large eye facing upwards. Meanwhile, the smaller, downward-facing right eye is probably specialized for detecting point-source bioluminescence in the darker waters below.

10.3 Do mesopelagic cephalopods need to be visually cognitive? Is there evidence to suggest that they are?

Much emphasis has been placed on the large brains and well-developed sense organs in cephalopods as adaptations for their ‘high performance’ lifestyles (Budelman, 1994, 1995). They are typically viewed as fast animals moving in complex environments, actively predating and evading predation, and often loosely social. However, as with many deep-sea taxa, the metabolic rate of deep-sea cephalopods is greatly reduced compared to their shallow water counterparts, likely a response to relaxed pressure from visual predation (Childress, 1995; Seibel & Carlini, 2001; Seibel, Thuesen, Childress & Gorodezky, 1997). Large brains are metabolically costly to maintain, and there is evidence in mammals that brain size will be reduced where lifestyle allows for it (Safi, Seid & Dechmann, 2005).

Godfrey-Smith (2002) described aspects of environmental complexity as an attempt to give a general functional explanation of cognition. He used the term cognition to describe ‘a collection of capabilities which, in combination, allow organisms to achieve



Figure 10.2 The lower-mesopelagic squid *Histeoteuthis* has asymmetrical eyes and optic lobes, with a large left eye for looking up for passing silhouettes of potential prey against the weak downwelling light, and a small right eye orientated downwards, probably specialized for detecting point-source bioluminescence. See plate section for colour version.

certain kinds of coordination between their actions and the world' that 'has the function of making possible patterns of behaviour which enable organisms to effectively deal with complex patterns and conditions in their environments'. In their consideration of body pattern richness and habitat complexity (see below), Hanlon and Messenger (1996) describe the pelagic realm as a uniform habitat, and it seems reasonable to accept that the open ocean contains less structural complexity than a near-shore reef habitat. However, if we use habitat to include the wider physical and biological characteristics of a species' interactions, then we must consider what habitat complexity means on an individual species basis. Given the characteristics of the mesopelagic realm, is there sufficient selective pressure for the evolution or maintenance of higher-level visual processes?

Complex behaviours and corresponding large brains tend to evolve in response to the selective pressure of complex ecologies, including trophic and social interactions (Lefebvre & Sol, 2008). Brain areas that receive direct input from sensory systems or are responsible for complex cognitive function are under strong selective pressure, with neural development often reflecting these behavioural adaptations and sensory specializations. For example, in primates both an increasing reliance on frugivory (indicating complex foraging behaviour) and social group size (indicating social complexity) are independently positively correlated with the size of the neocortex brain region. Research from multiple vertebrate groups, for example primates (Barton & Harvey, 2000), cichlid fish (Pollen et al., 2007) and bats (Safi & Dechmann, 2005), suggest that the cognitive centres in the brain are under specific pressure according to mosaic theory, whereby localized changes in functionally distinct regions are mediated by selection on a specific set of behaviours according to a given species' ecology (Barton & Harvey, 2000). In a comparative analysis controlling for phylogeny, bat species foraging in complex habitats, which must distinguish prey from background noise whilst avoiding obstacles, were shown to have larger brain regions associated with hearing and memory than species that hunting in open spaces (Safi & Dechmann, 2005).

Neuroecology is the study of the adaptive variation in cognition and the brain, often by employing behavioural and anatomical techniques to examine the neural correlates of cognition (Sherry, 2006). There are few studies directly investigating the correlation between pelagic versus benthic ecologies and brain structure independent of phylogeny. Yopak (2012) reviewed the neuroecology of cartilaginous fishes and found, irrespective of phylogenetic history, larger brains with well-developed telencephala and highly foliated cerebella occurred in reef-associated species, suggesting brain structures may have developed in conjunction with enhanced cognitive capabilities. In contrast, deep-sea species had relatively smaller brains, which the author suggested might be indicative of specialization of non-visual senses.

Maddock and Young (1987) measured 30 optic and chromatophore lobes of the brains of 63 species of cephalopod from all types of habitats, providing the most comprehensive data on the neuroecology of cephalopods currently available. However, this study did not control for phylogeny, meaning phylogenetic effects may confound the observed differences and similarities between taxa. We can nonetheless identify some general trends in the correlation between habitat and brain regions associated with vision and body patterning (Figure 10.3). These data suggest that the mosaic theory proposed for

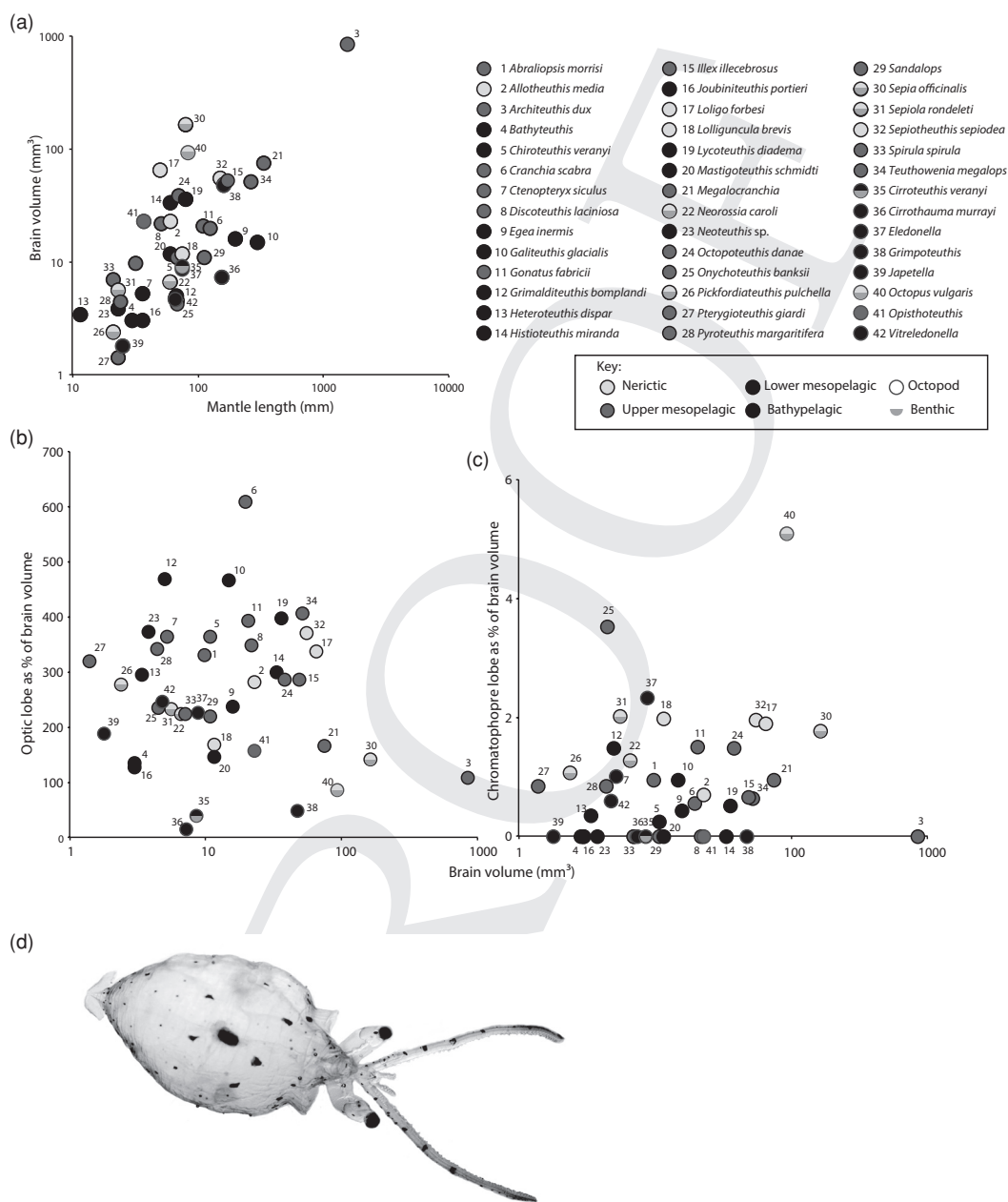


Figure 10.3 Brain size and brain regions in a range of cephalopods from different habitats (data taken from Maddock & Young, 1987). The 34 species of decapods plotted on each graph are listed on the right in alphabetical order. A further eight species of octopods are then listed in alphabetical order and are distinguished by a red marker ring. Numbers relate to the placement on the plot. The colour of marker represents a common habitat type (or usual collection depth range) for adults during daylight hours (the depth occurrence of many species changes with size and life-stage, and many of the species listed undergo vertical migration so will be found in shallower waters at night), as given in the key. (a) Absolute brain volume plotted against mantle

mammalian brains (Barton & Harvey, 2000), maybe be relevant for cephalopods; specific brain regions apparently associated with particular ecologies have a greater volume than would be accounted for by allometric scaling. In Figure 10.3 we show these data for 42 of these species for which complete records for mantle length, absolute brain volume, optic-lobe volume and chromatophore-lobe volume were given.

10.4 Body pattern repertoire in the open ocean and deep sea

For shallow-water cephalopods there is a clear link between vision and body patterning via the expression of chromatic components; there is no doubt that the visual system of species such as *Sepia officinalis* plays a vital role in making decisions about what body pattern to use in order to achieve effective camouflage in a given environment (see chapter 9, this volume, by Zylinski & Osorio). Hanlon and Messenger (1996) put forward a hypothesis of ‘ecological correlates of body patterning’ (ECBP) that suggested a strong correlation between habitat complexity and patterning richness (number of chromatic components). They proposed that diurnal cephalopod species occurring in complex habitats such as coral reefs or kelp environments have a richer array of body patterns at their disposal than near-reef or ‘murky habitat’ species, with a positive correlation between the two. With this correlation they extrapolated and predicted that species in the less-complex ‘open ocean’ habitat would have the lowest number of chromatic components, but conceded: ‘we can only make educated guesses about species living on the deeper continental shelf, the deep fore-reef, on bland substrates like mud or in oceanic and deep-water habitats’.

Accepting that Hanlon and Messenger’s (1996) ECBP was presented as a first attempt to develop the correlation between habitat and body pattern richness, it should be noted that it overweighs the significance of this correlation, because it assumes phylogenetic independence between the data points. In other words, the correlation between patterning richness and habitat complexity may be an artifact of the fact that most of the species for which data exists are closely related. For example, of the 12 coral reef, rocky reef or kelp environment species included, four are from the genus *Octopus*, while all of the ‘social

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Figure 10.3 (cont.) length, showing a positive correlation between brain volume and body length, although there is a tendency for shallow-water benthic taxa (namely *Loligo*, *Sepia* and *Octopus*) to fall above the trend, and bathypelagic/bathybenthic species to fall below the trend, be they octopod or decapod (note log scales). (b) Plotting optic lobe volume (given as a percentage of brain volume, measured separately because of location and large size (d)) against absolute brain volume shows that optic lobe volume varies greatly and is not correlated with overall brain volume. Interestingly, many pelagic and mesopelagic species have comparatively larger optic lobes than neritic/benthic species that are considered highly visual. (c) Plotting the chromatophore lobe volume against brain volume shows chromatophore lobe volume varies greatly between species. There is a trend for shallow-water species to have relatively larger chromatophore lobes, with notable exceptions (e.g. the deep-water pelagic octopod *Eledonella*). Many deep-sea species had no chromatophore lobes or lobes too small to be measured. (d) An oegopsid squid paralarva showing eye stalks with the large optic lobe located behind the eye on the stalk and separate from the brain. See plate section for colour version.

squids near reefs' are loliginids. It might, therefore, be that the common ancestor of *Octopus* had a richer range of body patterns compared with the common shared ancestor of *Loligo* and, therefore, the apparent trend between body pattern number and habitat could be largely explained by relatedness rather than by habitat complexity. A more thorough investigation using independent contrasts would correct for this (Felsenstein, 1985; Purvis & Rambaut, 1995; Seibel & Carlini, 2001). However, before this can prove useful we need to greatly increase and improve our knowledge and expand our data set with quality behavioural and physiological data, particularly for mesopelagic and bathypelagic taxa. Furthermore, while headway is being made in resolving phylogenetic relationships within the cephalopods, these are (not surprisingly) biased towards neritic taxa at the species level.

An important consideration for future work assessing the correlation between habitat and body pattern richness is defining sensible and applicable metrics for habitat complexity and chromatic components/body pattern richness. As Packard and Sanders (1971) pointed out: 'if we ask "How many patterns are there in an octopus?" the best, though hardly satisfactory, answer is, "There are as many patterns as can be recognized by the classifier"'. The large research effort on the body patterning of *Sepia* compared to any other group is unsurprising given the extraordinary camouflage capabilities of these animals (Hanlon, 2007; Zylinski & Osorio, 2011), but it has the potential to outweigh the number of chromatic components used by *Sepia*. Additionally, much work on *Sepia* has been carried out under controlled laboratory conditions (this said, we still have an incomplete description of their body patterning; see chapter 9, this volume, by Zylinski & Osorio). Conversely, observations in mesopelagic taxa (see below) are typically made from video footage under ROV lights, resulting in problems discriminating true physiological changes under artificial lighting, rapid changes in body position and unnatural behaviours. Issues such as these make sensible comparisons of body pattern richness between species difficult. At a more basic level, the ECBP as it stands considers only the structural aspects of the tangible environment; as discussed above, a more typical definition of a species' habitat includes all aspects of physical and biological conditions. While habitat *structural* complexity might drive a diverse range of body patterns for camouflage, social interactions might drive a wider range of body patterns for communication.

10.5 Evidence for complex visual behaviours and body patterning in mesopelagic cephalopods

10.5.1 *Octopoteuthis deletron*

Bush, Robison and Caldwell (2009) used ROV footage from Monterey Bay Aquarium Research Institute's (MBARI's) video archive (which records the occurrence of taxa filmed during the Institute's ROV deployments) to analyze the behaviour of the large pelagic squid, *Octopoteuthis deletron*. They analyzed observations of 76 (presumed) individuals recorded at depths between 344 and 1841 m and produced an ethogram of behavioural components that were displayed by more than one individual. These included

17 light and dark chromatophore-based components (see chapter 9, this volume, by Zylinski & Osorio and Hanlon & Messenger, 1996), some of which are surprisingly complex given the low-light environment, such as fine arm bands and ventral mantle bands. In addition to these chromatic components, the authors described a further 42 postural and bioluminescent components, giving a total of 59 components. This number is comparable to those for several neritic and reef squid for which ethograms exist, for example 59 in the broadfin squid *Sepioteuthis affinis* (Mauris, 1989), 39 in *Loligo opalescens* (Hunt, Zeidberg, Hamner & Robison, 2000) and 56 in *Loligo pealeii* (Hanlon, Maxwell, Shashar, Loew & Boyle, 1999). Bush, Robison and Caldwell (2009) suggest these behavioural components might serve to impede search image formation, disrupt hydrodynamic signatures and camouflage via Disruptive colouration and illumination, as well as being used in conspecific communication and offensive behaviour..

10.5.2 *Dosidicus gigas*

Following the study of *Octopoteuthis* by Bush, Robison and Caldwell (2009; see above), L. Trueblood, B. H. Robison and B. A. Seibel (unpublished data) used footage from the MBARI's ROV video library to produce an ethogram of behaviour and body patterning of the Humboldt squid *Dosidicus gigas* at depths greater than 150 m. They described 29 putative chromatic components as well as 15 postural components and 6 locomotory components. The authors suggest that of the 29 chromatic components described, 15 contained body countershading elements, making camouflage an important role in body pattern usage. Individual squid were observed to use chromatic component changes when aggregated than when solitary, suggesting that body patterning is used intraspecific communication in this species..

10.5.3 *Taningia danae*

Kubodera, Koyama and Mori (2007) used a mid-water high definition baited camera rig to record footage of the large eight-armed squid *Taningia danae* 'hunting' for suspended bait between 240 m (night) and 940 m (day). They did not report any body pattern colouration changes, but did observe arm-tip bioluminescence emissions associated with bait attacks. The authors suggest these might function to both blind prey and provide illumination to accurately determine target distance.

10.5.4 *Japetella heathi*

The pelagic octopus *Japetella* is caught in deep day trawls, with smaller individuals occurring in shallow waters (600–800 m) and mature adults in deeper waters (800 m+) (Roper & Young, 1975). This sluggish creature looks like a gelatinous ball with small arms – very different from the fast-moving, protean octopuses we are familiar with. However, we recently found that not all aspects of this small octopus are as slow as they first appear. These animals are rather transparent when left undisturbed (with reflective guts and eyes that are often associated with transparency), but are capable of expanding a layer of red–orange chromatophores over the mantle (Zylinski & Johnsen, 2011; Figure 10.4).

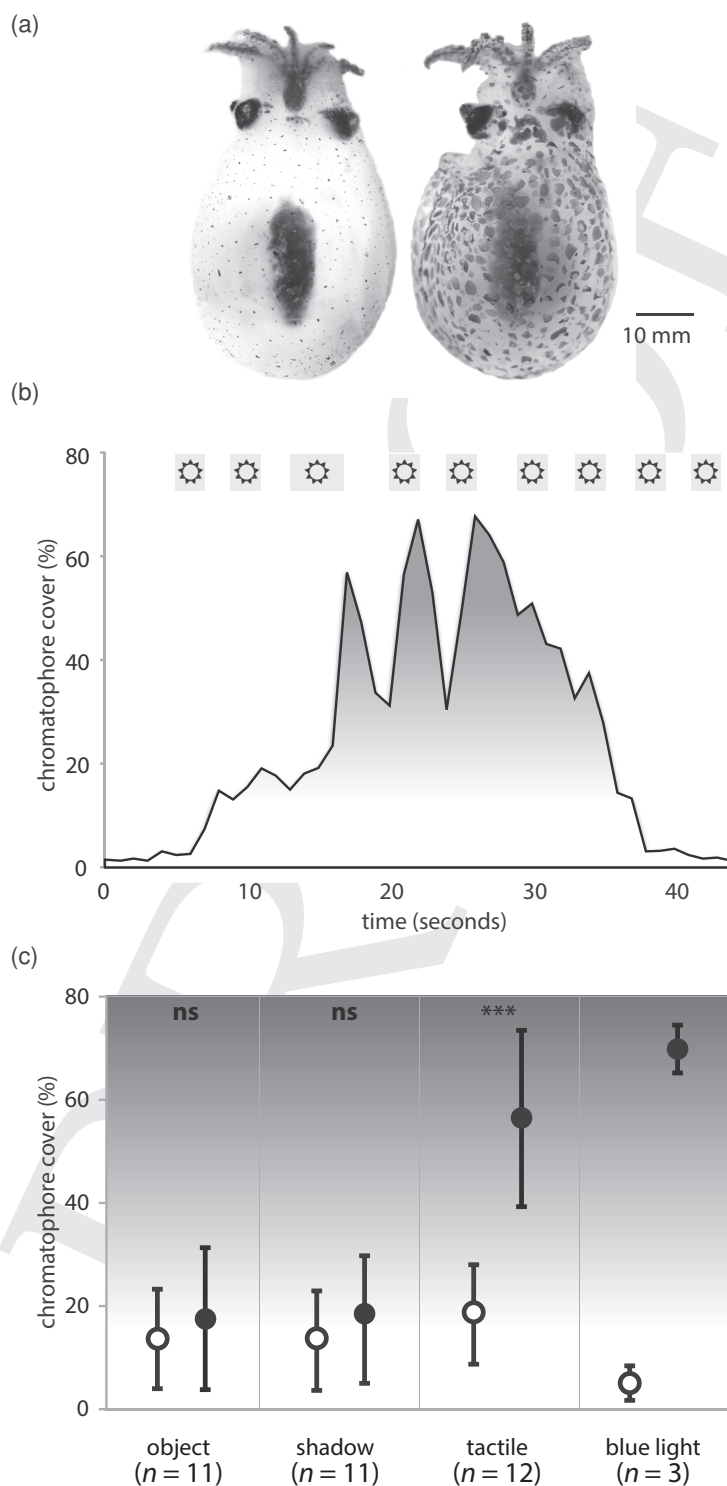


Figure 10.4 (a) The same individual *Japetella heathi* octopus in transparent mode (left) and pigmented mode (right). (b) Responses of a single *J. heathi* to directed blue light. Yellow boxes

We found that, while shadows and passing objects did not elicit the expansion of chromatophores in *Japetella*, a sudden onset of blue light caused these red-orange chromatophores to be expanded. This is consistent with the hypothesis that these and other cephalopods (e.g. *Onychoteuthis banksii*) can maintain camouflage under both ambient light conditions and bioluminescent searchlights. Interestingly, we found that they tracked passing objects, an observation made possible by their prominent, swiveling eyes. Sweeney, Haddock and Johnsen (2007) suggesting that *Japetella* may have poor visual acuity compared with other measured pelagic cephalopods. However, at four cycles per degree, this is comparable to the acuity of a rainbow trout, which seems rather good for an animal assumed to have very little visual stimulation within its habitat, and which appears to have limited abilities to evade or respond to visual threat compared with the rapid responses typical of many cephalopods.

10.6 Bioluminescence: using and detecting

In their discussion of ecological correlates of body patterning Hanlon and Messenger (1988) stated: ‘We might . . . predict that cephalopods with light organs inhabiting the oceanic mid-waters could signal with bioluminescent body patterns’. As the intensity of the ambient downwelling light decreases, the occurrence and importance of bioluminescence increases. At depths greater than around 800 m (the exact depth being defined by local conditions) bioluminescence becomes the dominant source of light (Young, 1983), present in every major taxonomic group represented. Haddock, Moline and Case (2010) discuss the functions, diversity and physiology of bioluminescence in an excellent review, and we direct the interested reader to this. Here, we draw attention to the fact that almost half of cephalopod genera (66 of 139) possess bioluminescent organs (Hastings & Morin, 1991), and a vast majority of the taxa possessing such organs are mesopelagic (Figure 10.5). A well-known exception to this is the near-shore sepiolid squid *Euprymna scolopes*, which produces bioluminescence via the luminescent bacterial symbiont *Vibrio fischeri* (Ruby, 1996). The apparent functions of bioluminescence in cephalopods are varied, including sexual signalling, biological searchlights, counterillumination and

Figure 10.4 (cont.) and icon indicate onset and cessation of individual lighting ‘bouts’, consisting of a flashing blue light at one flash per second. Most bouts lasted for 3 seconds and, therefore, subjected the animal to three flashes. Chromatophores can be seen to expand seconds after initial exposure. After continued exposure the animal ceased reacting to the light with chromatophore responses, and instead displayed evasive behaviour such as swimming away from the light-source and retraction of the head into the mantle. (c) Responses of *J. heathi* to four different stimuli. Objects passed in front of the animals, and shadows passed overhead, failed to evoke a significant increase in chromatophore expression. A tactile stimulus (touching the arms with a blunt needle) resulted in the rapid expansion of chromatophores. By comparison, directed blue light resulted in a rapid and strong expression of chromatophores. White circles = pre-stimulus, black circles = post-stimulus. Error bars show standard deviation from mean. See plate section for colour version.

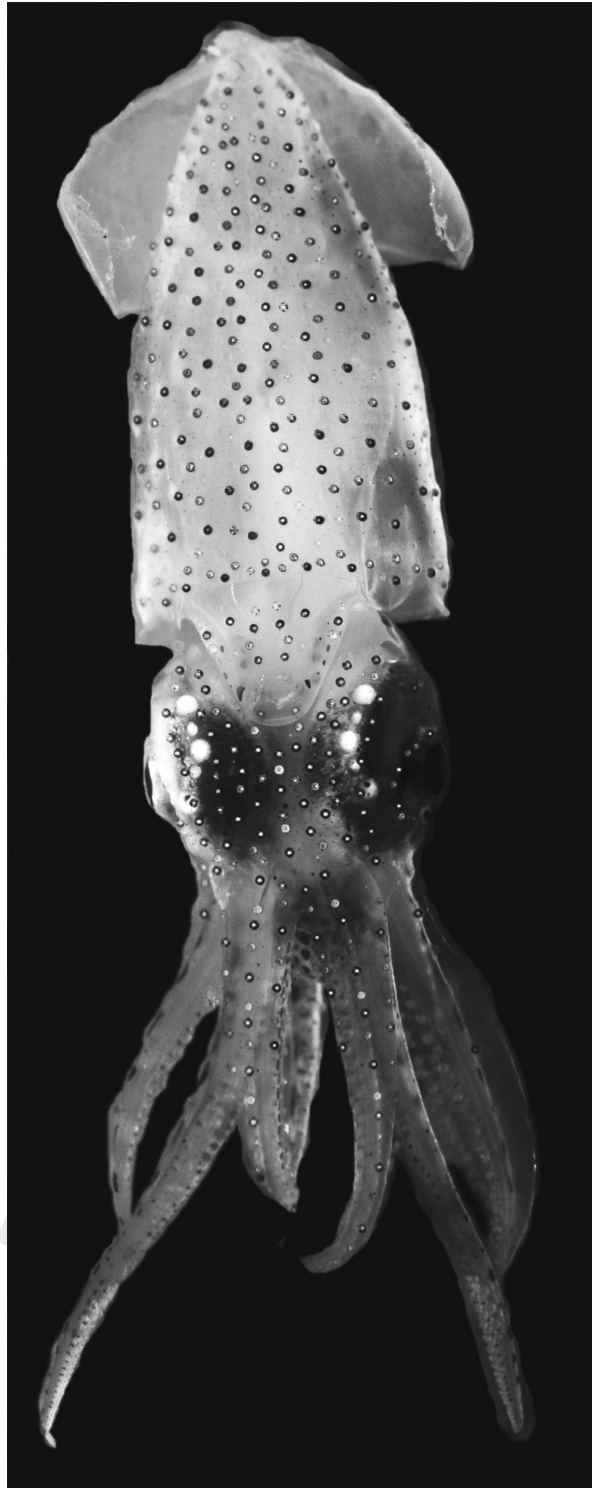


Figure 10.5 Ventral and ocular photophores on the ventral surface of an *Abraliopsis* squid. See plate section for colour version.

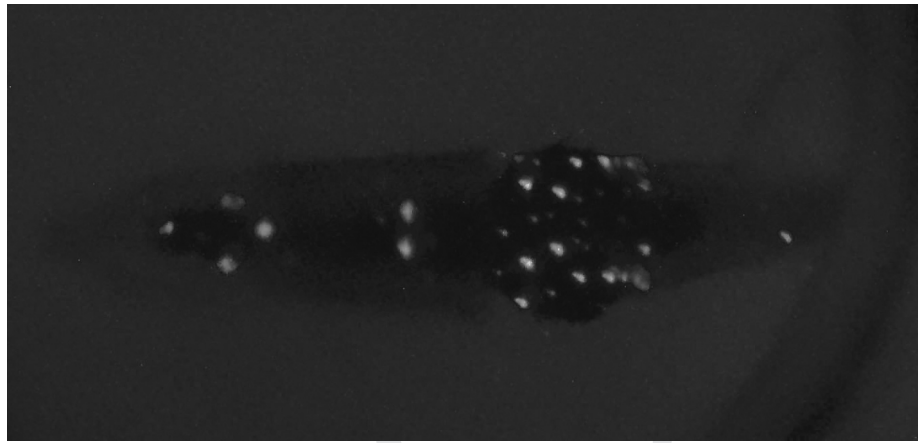


Figure 10.6 Counterilluminating photophores in the squid *Pterygioteuthis*. Here, during shipboard experiments, the very low downwelling blue light was turned off and the animal photographed from below under dim red light.

hunting behaviour (Clarke, 1963; Haddock, Moline and Case, 2010; Johnsen, Widder & Mobley, 2004; Johnsen, 2005; Young, 1978, 1983). Bioluminescence seems to have evolved multiple times in cephalopods, with some species utilizing symbiotic luminescent bacteria (e.g. *Euprymna*), while most deep-sea taxa have intrinsic bioluminescence.

Counterillumination is an important function of bioluminescence in pelagic cephalopods (Johnsen, Widder & Mobley, 2004; McFall-Ngai, 1990; Widder, 2010). Many predators visually hunting in the mesopelagic have upward-pointing eyes positioned to take advantage of the conspicuousness of the silhouettes against the downwelling ambient light. Many animals get around this by being transparent, which provides the advantage of being effective from all viewing angles. Yet this is not a complete solution to camouflage in the pelagic (see section 10.5.4. on *Japetella heathii* above). Another solution is to use counterilluminating photophores that obliterate a silhouette by emitting light at the wavelength and intensity of the downwelling light from ventral photophores (Figure 10.6). Many cephalopods have extra-ocular photosensitive vesicles, which are presumed to play a role in determining the output of ventral photophores. Young (1978) conducted shipboard experiments where they used opaque ‘shutters’ to block information about the intensity of downwelling light to a species of *Abraliopsis* squid over the dorsal photosensitive vesicles, the eyes, or both. They demonstrated that the intensity of the ventral photophores was independently affected by covering both eyes and photosensitive vesicles, but that the latter had a greater effect. It would be interesting indeed to know how information regarding downwelling light and the intensity of the photophore output is processed.

The deep sea is often considered to be a lightless environment, but biological light provides a method for communication that has the potential to be information rich as well as spatially and temporally complex. Matching the spectral and intensity characteristics of the ambient downwelling light for counterillumination is non-trivial. These are two

potential ways in which bioluminescence could support complex visual processing in the pelagic realm.

10.7 Concluding remarks

Gaping holes exist in our knowledge of the basic behaviour of most cephalopods, many of which inhabit the vast, three-dimensional wilderness that is the deep sea. Gaining insight to potential complex behaviours in mesopelagic taxa is difficult for numerous reasons.

The need for a wide body pattern repertoire for camouflage via chromatic components is reduced in the mesopelagic realm. Body patterning is probably less useful at depth for two main reasons: (1) light is more monochromatic; and (2) the visual resolution of most animals is far worse due to spatial summation. Although camouflage is still important, it is more commonly achieved in deep-sea cephalopods by passive means, such as reflectors, transparency (Figure 10.7) or overall red/black colouration. Counterillumination via bioluminescence to obliterate silhouettes must match the ambient downwelling light in order to be effective, and the means by which this is achieved is not well understood. However, it seems unlikely it will require cognitive processes in the traditional sense. Cognition is needed is when adaptive responses depend on changing conditions. When an environment is highly constant – such as the deep sea – there is no selective pressure for cognitive responses, as fixed responses are sufficient. In addition the environment is colder, darker and food-limited, meaning that visual cognition and the brainpower needed to mediate it are unlikely to evolve.

At present, attempts to correlate body pattern richness with habitat (or environmental) complexity seem fraught with difficulties of assessing either in a comparable or repeatable way. Pelagic habitats from well-lit surface waters to deep, cold waters, although indeed equally low in habitat (structural) complexity, perhaps offer more variable and complex environmental conditions than is often appreciated. A metric of complexity that accounts for interactions with conspecifics and predators, the level of usable ambient light, the degree of bioluminescence available for visual tasks and factors regarding metabolic constraints should be developed to enable comparisons between pelagic species. Similarly, phylogenetic relatedness may be a confounding factor in apparent correlations between body pattern richness and habitat complexity, and between body patterning and visual cognition.

Chapter 9 of this volume (by Zylinski & Osorio) introduced concepts about what makes vision cognitive, and emphasized that internal representation is likely an important determinant here. The lack of a body pattern output that directly relates to aspects of the visual environment in mesopelagic taxa invalidates the use of this assay for evidence of internal representation. Many aspects of the ecology and physiology of a majority of mesopelagic cephalopod taxa lead us to doubt the need or presence of cognitive vision. However, ROV footage of some species suggests complex behaviours and a surprisingly large body pattern repertoire. Furthermore, brain measurements show a large investment in optic lobes (coupled with large eyes) and learning centres (e.g. the

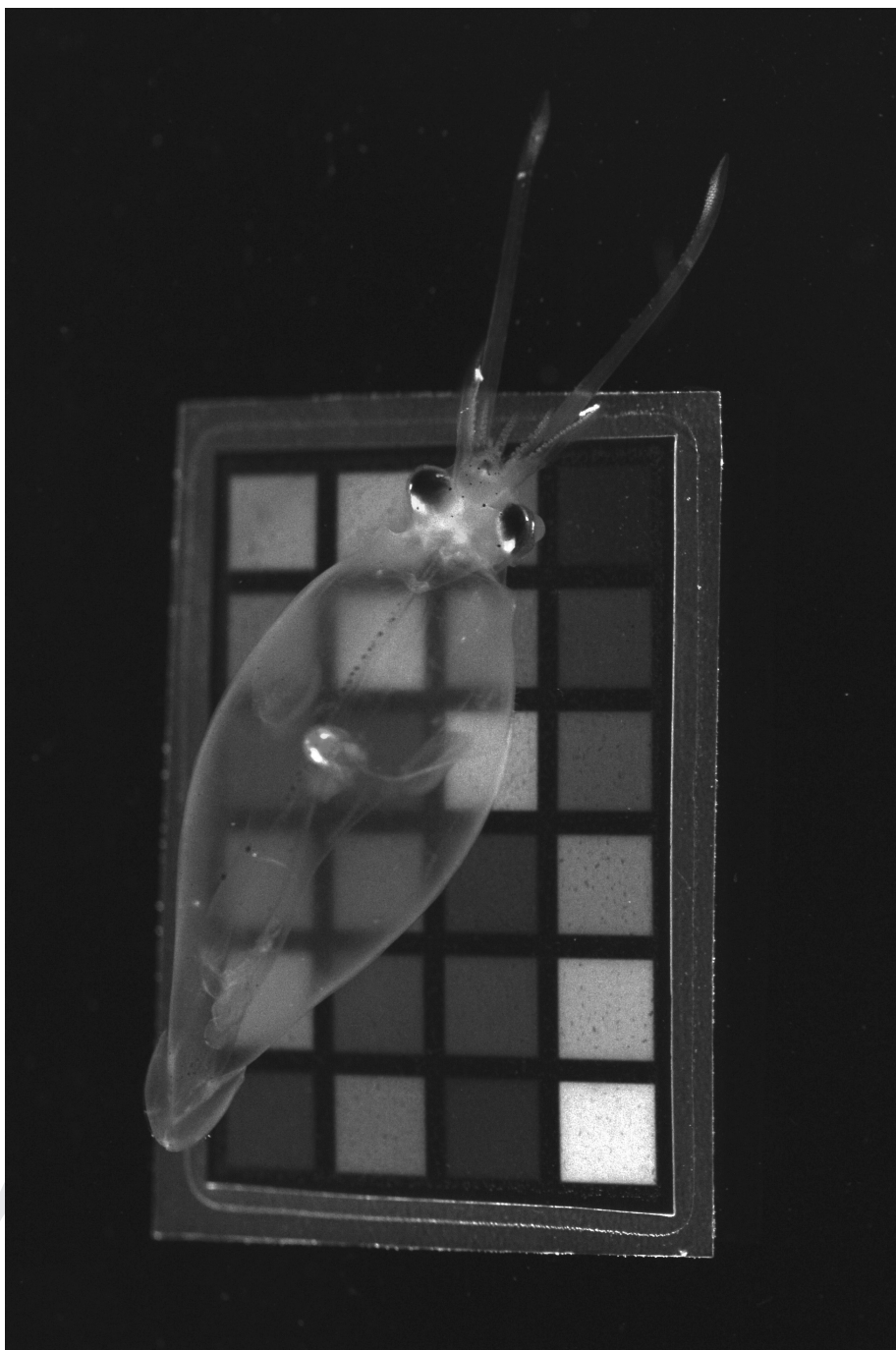


Figure 10.7 Transparency is a common form of camouflage in the mesopelagic realm. Here the transparency of a chryseid squid is demonstrated as it rests over a colour standard. See plate section for colour version.

vertical lobe system) in some taxa, which tantalize us with the potential for complex visual processing. Finally, the complex species-specific photophore patterns found in many mesopelagic squids provide another avenue for visual communication that is so far poorly understood.

Chapter 9 of this volume (by Zylinski & Osorio) highlights similarities between visual processing in the neritic cuttlefish *S. officinalis* and vertebrates (including humans). The visual environment in the well-lit shallow-water benthic environment is not dissimilar to our own visual world in many respects, and the body patterns used by *S. officinalis* for camouflage are designed primarily to defeat shallow-water vertebrate (including mammalian) predators. It is, therefore, perhaps unsurprising that evolution has provided similar solutions to shared problems. In contrast, it is harder to imagine the visual tasks facing cephalopods and their predators in a low-light world where biological light might be the most important source of illumination. We hope time and research effort will shed light on this. As new technologies allow us better access than ever to the world's largest and least understood habitat we will surely be treated to many more fascinating cephalopod stories. Whether visual cognition is ultimately an interesting avenue of research to pursue for majority of these taxa, any behavioural data obtained can only be an asset given the current level of knowledge.

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